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Interactions between microorganisms and soil invertebrates in nutrient flux pathways of forest ecosystems

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Introduction

A fairly comprehensive body of information is available about the structure and functioning of forest ecosystems (Reichle, 1981), which, together with the widespread application of watershed techniques, has emphasized the role of soil biological processes in regulating the dynamics and conservation of nutrients in these systems. In particular, the key processes of nutrient immobilization, mineralization and release not only determine the availability of elements for root uptake but, at a gross level, regulate the response of the ecosystem to perturbations such as insect attacks (Zlotin & Khodashova, 1980) or the catastrophic effects of fire, wind-throw or clear-felling (Woodmansee & Wallach, 1983; Tamm, Holmen, Popović & Wiklander, 1974; Vitousek & Melillo, 1979; Khanna, 1981). The balance between nutrient immobilization and mineralization in relation to rates of accession may also be critical for the accumulation of a nitrogen capital sufficient to support a forest ecosystem (Reiners, 1981; Bradshaw, Marrs, Roberts & Skeffington, 1982); alternatively accumulation may represent effective removal of available nutrients from short-term cycles with the possibility that primary productivity becomes limited as the stand matures (Miller, 1979).

The functioning of decomposition and nutrient cycling processes at this gross level is reasonably well understood in natural ecosystems and this knowledge has been applied to watershed management and forestry

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practices (Swank & Waid, 1980; Aber, Botkin & Melillo, 1978, 1979; Miller, 1981). There has, however, been little explicit recognition of the complexity of the processes which regulate nutrient fluxes between litter, soil and plant roots in forest ecosystems (Frissel & Van Veen, 1982), and no general recognition, let alone quantification, of the involvement of soil invertebrates in these processes. The behaviour of nitrogen, for example, is frequently interpreted in terms of simple hypotheses based on one or two processes developed for agricultural systems (Heal, Swift & Anderson, 1982). There is evidence to support the concept of critical carbon : nitrogen ratios in agricultural soils (Scarsbrook, 1965; Alexander, 1977; Paul & Juma, 1981) where organic matter inputs tend to be high in nitrogen, low in lignin, and are associated with relatively homogeneous mineral soils with high bacterial activity. However, there are good reasons for supposing that the general concept may be inadequate to explain nitrogen dynamics in forest soils where litter has a low quality and the time course of decay is protracted; in these conditions there is an increased probability of nitrogen immobilization in intractable organic compounds (Heal, Swift & Anderson, 1982). A number of new models have been proposed relating the timing of nitrogen release to the initial nitrogen content and decomposition rate of litter (Aber & Melillo, 1982; Bosatta & Staaf, 1982), but the rationale is based entirely on microbial processes. Bosatta & Staaf (1982) specifically assume, as a requirement of their model, that fauna have insignificant roles in nutrient mobilization in coniferous and many other forest ecosystems.

It is axiomatic from the trophic organization of decomposer communities that soil invertebrates will interact with fungi and bacteria in nutrient flux pathways between decomposing organic matter and plant root systems. The functional level at which it is necessary to take account of animal–microbial effects in understanding the mechanisms of nutrient cycles is unclear, though it will certainly vary between systems and individual processes.

The central problem is quantifying both the direct and indirect effects of invertebrates on soil processes in a way that may be integrated into ecosystem models or nutrient budgets. The direct effects involve transfers between pools where the fluxes are mediated directly by animals. Thus saprophagy, bacteriophagy, mycophagy, and necrophagy (carnivory) will involve the release of nutrients through feeding activities, excretion and turnover of secondary production. The indirect effects involve feedbacks to lower trophic levels; for example, the effects of comminution and grazing on microbial activity and functional organization of bacterial and fungal communities, and the effects of predators on the population dynamics of their prey.

We will therefore firstly consider some of the evidence for the role of soil invertebrates in mineral element fluxes, identifying direct and indirect effects on microorganisms where possible; then attempt to quantify the process variables and, finally, consider the mechanisms involved in animal–microbial interactions.

This review is largely confined to considering the role of mesofauna and macrofauna in mineral element release from forest leaf litter and soil organic matter in view of the contributions by Swift & Boddy (Chapter 4) and Coleman, Ingham, McClellan & Trofymow (Chapter 2).

Direct effects of animals on nutrient fluxes

There is a very extensive literature on the role of soil animals in nutrient flux pathways of grassland and forest ecosystems which is covered by numerous symposia and review volumes; for example, Doeksen & van der Drift (1963), Vaněk (1975), Anderson & Macfadyen (1976), Dickinson & Pugh (1974), Lohm & Persson (1977).

The general approach to quantifying the direct contribution of animals to nutrient cycles is to budget mineral element transfers involved in the trophic and population dynamics of the fauna; see, for example, Edwards, Reichle & Crossley (1970), Reichle (1977), Anderson, Coleman & Cole (1981), Krivolutsky & Pokarzhevsky (1977), Persson *et al.* (1980), Persson (1983). Results of a number of studies suggest that in temperate soils with a faunal biomass of at least 5–10 g dry wt m^{-2}, the annual turnover of elements by the fauna can equal or exceed element inputs in leaf litter to the decomposer system (Satchell, 1963; Graff, 1971; Zajonc, 1971; Zlotin, 1971; Zlotin & Khodashova, 1980; Krivolutsky & Pokarzhevsky, 1977; Stachurski & Zimka, 1977).

The majority of studies calculate nutrient losses from a year class of litter and do not place the results within the context of an ecosystem budget. Syers, Sharpley & Keeney (1979) calculated that the contribution of earthworms to nitrogen mineralization in a New Zealand pasture was small in relation to *in situ* microbial mineralization of nitrogen in litter, and that the activities of the worms were insignificant in relation to the overall turnover of nitrogen in the ecosystem. The contribution of earthworms to this budget, however, is based on the mineral nitrogen content of *Lumbricus rubellus* casts. Since this is not predominantly a surface casting species (Edwards & Lofty, 1977) the direct effects of the worms on nitrogen mineralization, let alone the indirect effects on microbial activity, are probably underestimated.

Few of these studies differentiate between litter and microbial pools and it is therefore impossible to assess the comparative importance of the animal–microbial interface in these nutrient fluxes. There is circumstantial evidence from litter-bag experiments that the feeding activities of the microfauna (Protozoa and nematodes) and mesofauna (Collembola and mites) are more important in mobilizing nutrients than contributing to weight loss from leaves (Wood, 1974; Seastedt & Crossley, 1980; Anderson, Proctor & Vallack, 1983) but few field studies exist where this effect has been quantified.

One of the most detailed analyses of the trophic structure and biomass dynamics of soil organisms is a study on a 120-year-old Scots pine (*Pinus sylvestris*) forest in Sweden carried out by Persson *et al.* (1980). Northern coniferous forests normally have a much lower soil fauna biomass than 5–10 g m^{-2} and it could be argued that the effect of the animals might be insignificant in relation to the biomass and activity of the microorganisms. Persson *et al.* (1980) calculated that although the soil fauna represented a biomass of only 1.7 g m^{-2} (in comparison with 120 g m^{-2} fungi and 39 g m^{-2} bacteria) and contributed only 4% of heterotroph respiration, they consumed 30–60% of microbial production in the litter and humus layers of this site. As a consequence of this the soil invertebrates directly contributed between 10 and 49% of total nitrogen mineralization (28 kg ha^{-1} yr^{-1}) (according to the value of nitrogen assimilation efficiency assumed in the model), of which 70% was excretion by bacterivores and fungivores.

Ausmus, Edwards & Witkamp (1976) also used a budgetry approach in investigating fluxes of carbon, nitrogen, phosphorus and potassium through the soil microbiota in a warm temperate deciduous forest in Tennessee (USA). Element concentrations were measured over one year in litter fall, roots, atmospheric inputs, fauna, microorganisms, leachates and soil organic matter. Highest levels of microbial immobilization of nutrients occurred in summer, and lowest levels during the spring period of maximum root growth. Ausmus *et al.* (1976) concluded that the fauna were critical for mediating the nutrient transfers and that grazing of up to 86% of the fungal production by the fauna was a key process. Laboratory microcosm studies were cited as evidence of these interactions in which it was demonstrated that snails and millipedes were integral to the transfers of ^{135}Cs from litter to plant seedlings (Patten & Witkamp, 1967) and that a reduction of microbial biomass was involved in the mobilization of potassium and magnesium (Witkamp & Frank, 1969, 1970). However, no analyses were made for nitrogen or phosphorus in these experiments, although these elements are characteristically immobilized by microorganisms involved in litter decomposition (Swift, Heal & Anderson, 1979).

Anderson, Ineson & Huish (1983*a*) found that the addition of millipedes to decomposing leaves increased ammonium-N losses by up to sixteen times control levels. This effect did not occur step-wise with the addition of animals and, when the animals were removed, nitrogen mineralization only returned to control levels after a period of several weeks (Fig. 3.1). The implication of these results is that indirect effects of the animals are more important in nitrogen mineralization than their direct contribution through feeding or excretion.

Indirect effects of animals through interactions with soil microorganisms

The direct contribution of soil invertebrates to total heterotrophic metabolism varies from about 1% to 15% (Edwards *et al.*, 1970;

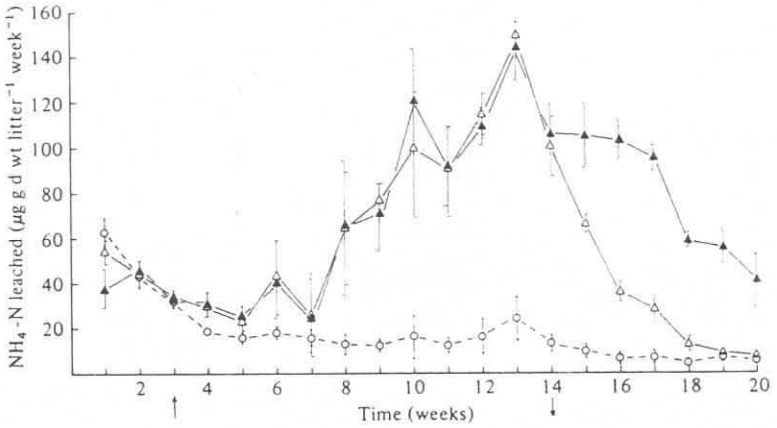

Fig. 3.1. The effects of adding and removing *Glomeris marginata* on ammonium-N release from oak leaf litter. Three sets of microcosms were set up containing 2 g dry wt oak leaf litter and incubated for three weeks at 15 °C before the animals (4 per chamber) were added to two treatments (▲, △). Controls (○) were maintained without animals. At week 14 the millipedes were removed from one of the animal treatments (△). Results are expressed as μg N g dry wt litter^{-1} week^{-1} ±1 SE; n = 4. (Anderson, Ineson & Huish, unpublished data.)

Reichle, 1977; Persson *et al.*, 1980), but their influence on microbial activity may be proportionally greater through the indirect effects of comminution, grazing and the dispersal of inocula (Macfadyen, 1963).

Standen (1978) found that experimental material held in mesh litter-bags enclosing Diptera larvae or enchytraeids had higher weight loss, attributable to greater microbial respiration, than control bags lacking animals. Laboratory experiments have shown, however, that the quantitative effects of animal feeding activities are complex and not predictable *a priori*. Woodlice and millipedes feeding on leaf litter were found to induce a non-linear response in microbial respiration with enhancement of up to 1.6 times control levels with optimal numbers of animals, yet at higher feeding intensities microbial respiration declined (Hanlon & Anderson, 1979). In addition, comminution may enhance microbial catabolism by increasing the surface area of the resource exposed to enzyme attack so that respiration is inversely related to litter particle size. Thus respiration increases in relation to the surface area to volume ratio of the resource, but the compaction of small particles into aggregates may inhibit fungal attack (Hanlon, 1981*a*, *b*). Scanning electron micrographs of artificial and faecal aggregates show that while bacteria are distributed throughout the comminuted litter, fungal hyphae are confined to the outer surface of the aggregate (Hanlon and Anderson, unpublished data). The results of these experiments suggest that the feeding activities of particular size groups of fauna may determine subsequent pathways and processes of decomposition, not only in the litter layers, but as the comminuted material is sorted by physical processes in the soil profile. The accumulation of finely particulate material in the humus layers might therefore result in inhibited decomposition and the immobilization of nutrients in a way which is not predictable from the original composition of the litter resource. Highly organic, moder humus-forms, where the soil organic matter is largely composed of microarthropod and enchytraeid faeces (Kubiena, 1953; Zachariae, 1965; Babel, 1972), can develop under tree species which produce litter readily attacked by soil animals and microorganisms in the litter layers (Anderson, 1973*a*). The causal relationship between litter comminution by mesofauna and the accumulation of soil organic matter is speculative but might be a gross manifestation of the phenomenon observed by Grossbard (1969) and others, that the faeces of cryptostigmatid mites appear to have a longer residence time in soils than the cellular structure of the parent litter from which they were derived.

Grazing involves the consumption of fungi and bacteria by microfauna or mesofauna which are of the size to select microbial tissues from the organic matter matrix. Their effects may therefore be very specific and can indirectly influence the composition and activities of the microbial community. A number of workers have demonstrated in the laboratory that protozoa and nematodes are able to regulate the growth dynamics of bacteria and hence the turnover and mineralization of nitrogen and phosphorus (Cole, Elliot, Hunt & Coleman, 1978; Anderson *et al.*, 1981; Bååth *et al.*, 1978, 1981; Clarholm *et al.*, 1981), and Coleman *et al.* (Chapter 2) suggest that microsite effects are of particular consequence in the rhizosphere.

Parkinson, Visser & Whittaker (1979) showed that grazing by Collembola may be species selective and that the differential effects of grazing intensities can alter the balance of fungal species in decomposing leaf litter. Newell (1980) also invoked grazing by Collembola to account for the microdistribution of *Mycena galopus* and *Marasmius androsaceus* mycelia in the soil profile; however, the functional consequences of these changes are unknown. Ineson, Leonard & Anderson (1982) showed that Collembola enhanced nitrogen mineralization in the early stages of litter decomposition but Visser, Whittaker & Parkinson (1981) found no evidence of grazing effects on nutrient release. On the other hand Seastedt & Crossley (1980) suggest that the stimulation of fungal growth by microarthropod grazing could lead to greater immobilization of nutrients. Similar conflicting effects of grazing on fungal biomass and respiration have been recorded (Hanlon & Anderson, 1979; Hanlon, 1981*c*; Addison & Parkinson, 1978; van der Drift & Jansen, 1977, and Bengtsson & Rundgren, 1983). The positive and negative responses of fungi to grazing may be reconciled by considering the growth dynamics of fungi and Collembola in leaf litter (Fig. 3.2*a*) in relation to nitrogen mineralization (Fig. 3.2*b*). In the ungrazed litter systems fungal development followed the classic growth curve exhibiting lag, exponential and stationary phases. In contrast, changes in fungal standing crop (living and dead material) were more complicated in treatments with animals, showing a stimulation of fungal growth (and reduced nitrogen losses) at low grazing intensities, similar to the results of Hanlon & Anderson (1979). At high grazing intensities, resulting from a population increase of Collembola after six weeks, a reduction in fungal standing crop occurred which was associated with increased nitrogen mineralization. Parkinson *et al.* (1979) and Hanlon & Anderson (1979) also observed that grazing rates may exceed the production of fungal hyphae, but the balance of these processes may be modified by the growth response of the fungus to increasing nitrogen concentrations (Park, 1976), the available nutrient supply (Hanlon, 1981*c*), and the food quality of the fungus for the Collembola (Booth & Anderson, 1979). The interaction of these variables in relation to the physical structure of the substrate has been demonstrated by Leonard (unpublished) using two- and three-dimensional bead matrices in which the fungus *Mucor plumbeus* was grown in media with defined nitrogen concentrations as asparagine, and grazed by the Collembola *Folsomia candida*. At a low nitrogen concentration (2 µg l^{-1}) the interaction was stabilized (Fig. 3.3*a*); the growth and reproduction of the Collembola

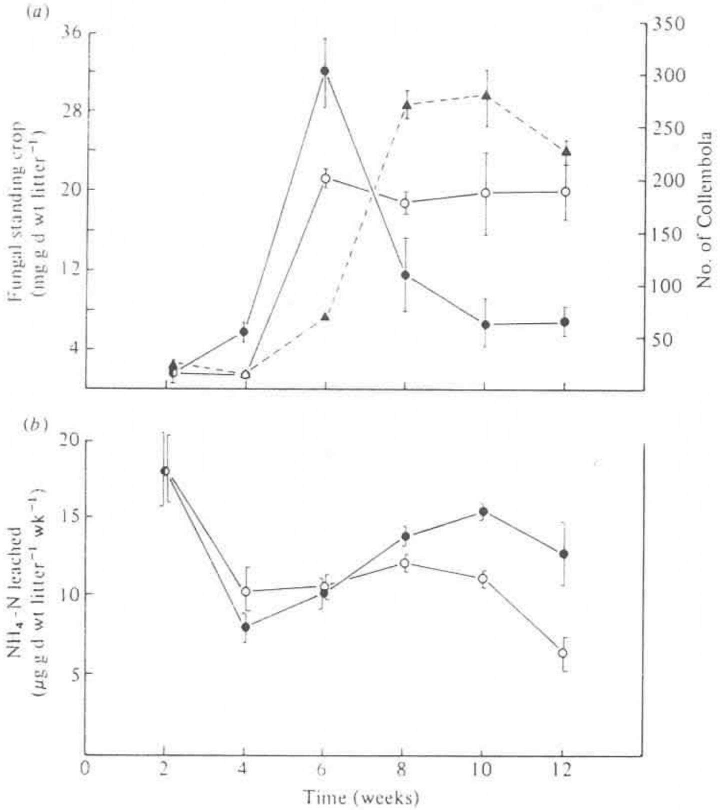

Fig. 3.2. (*a*) Fungal standing crop on oak leaf litter with (●) and without (○) the effects of grazing and changes in the Collembola populations (▲). (*b*) The mobilization of nitrogen, as ammonium, from grazed (●) and ungrazed (○) litter. Values shown are means ±1 SE; n = 4. (After Ineson, Leonard & Anderson, 1982.)

were more limited by the nutritional quality of the fungus than was the growth of the fungus by the quality of the medium. In the three-dimensional bead matrix, using the same amount and concentration of growth medium, the dynamics of collembolan and fungal growth were completely different: the Collembola population increased, where it had previously been static, and fungal growth was enhanced relative to ungrazed controls (Fig. 3.3*b*). The fungus used in these experiments showed an approximately linear growth response to increasing nitrogen, but further complexities of interaction would arise with fungi showing non-linear or negative responses to nitrogen concentration (Park, 1976). In addition to these specific effects on fungal growth, both grazing and comminution cause a gross shift from fungal to bacterial dominance in decomposing litter and soil organic matter (Hanlon & Anderson, 1979, 1980). An increase in bacteria on substrates associated with the feeding activities of mesofauna and macrofauna has been noted in many studies and is generally attributed to bacterial growth, both of ingested and endogenous gut microbiota, during the passage of material through the animal gut. This phenomenon is well documented for earthworms

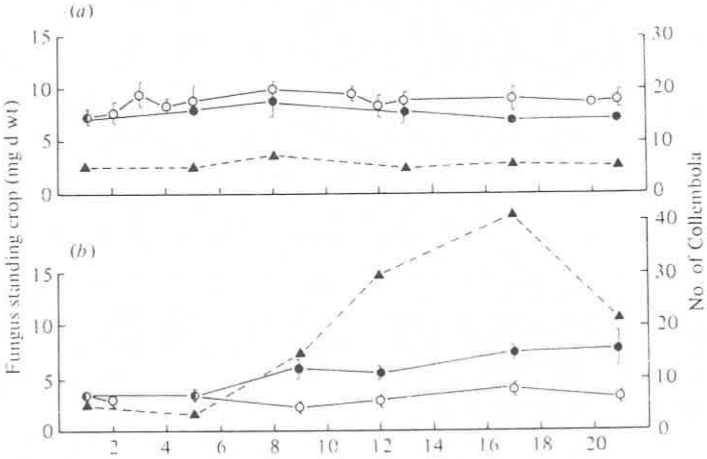

Fig. 3.3. The influence of spatial heterogeneity on the growth of *Mucor plumbeus* in (*a*) two-dimensional and (*b*) three-dimensional bead matrices with (●) and without (○) the effects of grazing by *Folsomia candida* populations (▲). The fungus was grown in a defined medium containing 2 mg l^{-1} N (as asparagine) and Collembola were added seven days after the fungal inoculum. Fungal mycelium was recovered by washing and sonic separation from the matrix, and the Collembola by floatation. Results are expressed as mean weight or counts per culture ±1 SE; n = 5. (Leonard, unpublished.)

(Ghilarov, 1963; Went, 1963; Parle, 1963; Atlavinyité & Lugauskas, 1971; Kozloskaja, 1971; Márialigeti, 1979) as well as for a wide range of arthropod groups including Diptera larvae (Szabo, Marton & Buti, 1969; Swift & Boddy, Chapter 4), isopods (Reyes & Tiedje, 1976; Anderson & Ineson, 1983), millipedes (MacBreyer, 1973; Anderson & Bignell, 1980; Anderson & Ineson, 1983; Szabo *et al.* 1983) and mites (Stefaniak & Seniczak, 1976). Thus, even in soils with low pH conditions where biological processes are considered to be dominated by fungi, the feeding activities of the soil fauna form a dynamic mozaic of microsites of intense bacterial activity.

Assessing the overall significance of soil invertebrates in nutrient cycles resolves on quantifying the indirect effects on animal–microbial interactions. The complexity of the processes involved precludes the formulation of a working model to evaluate their importance, but unless this can be done it is only possible to quantify the direct contribution of invertebrates to nutrient pools and fluxes. It is unlikely that this paradox will be resolved in the field at the organism–microsite level in the foreseeable future, and it is necessary to adopt an approach where processes and parameters are compartmentalized at a level where direct and indirect effects on nutrient transfers can be related to simple first order (empirical) variables.

This is essentially the value of the microcosm approach, defined by Patten & Witkamp (1967), where the components of a system can be studied at a realistic level of complexity and processes resolved into simple inputs and outputs from experimental materials in relation to specific treatments. There has been a proliferation of such microcosm studies during the 1970s, culminating in some extremely complex experiments carried out by Bååth *et al.* (1978, 1981), Clarholm *et al.* (1981) and Coleman *et al.* (Chapter 2). These studies have provided considerable insight into the dynamics of processes and mechanisms of animal–microbial interactions but cannot be quantitatively extrapolated into the field. The same limitations apply to our demonstrations of the effects of millipede and collembolan grazing on nutrient mobilization (Ineson *et al.*, 1982; Anderson *et al.*, 1983*a*).

Our current approach is to develop specific hypotheses for animal–microbial interactions in nutrient fluxes, which are testable in the context of processes operating in deciduous woodlands with acid, organic humus forms; particularly moders (*sensu* Kubiena, 1953) developed under sessile oak (*Quercus robur*), which is the commonest form of woodland system in Devon, UK. The effects of animals are measured in terms of minerals released into solution from litter and organic matter, where they are potentially available for root uptake. Such releases are related to simple process variables.

Process variables of animal–microbial interactions

Swift *et al.* (1979) identified the main variables of decomposition processes as the organisms (animals and microorganisms), resource quality (the physico-chemical attributes of the material), and the physical environmental conditions (particularly temperature and moisture) in which the organisms are acting. We use this framework for considering the process variables involved in animal–microbial interactions.

All the following experiments were carried out in chambers described by Anderson & Ineson (1982) which facilitate measurements of leaching losses from soil and litter materials in relation to animal treatments. Details of the preparation of materials and analysis are given in Anderson *et al.* (1983*a*). The experiments were designed to investigate the contribution of mesofauna and macrofauna to nutrient fluxes with nematodes and protozoa as uncontrolled variables.

Organisms: animal groups

The effects of a range of animal groups on nutrient mobilization from oak leaf litter were investigated by Anderson *et al.* (1983*a*) and the results are summarized in Table 3.1. Numbers of animals were chosen to demonstrate the maximum likely effects which might occur within aggregated field populations, and the results show that the animal treatments generally resulted in enhanced losses of all elements over controls, although individual effects for animals and groups were not significant in many cases. Animals had the most marked effect on ammonium fluxes, with increased leachate concentrations 10 to 20 times control levels for the millipedes and 60 times control levels for earthworms. The effects of Collembola and enchytraeids were comparatively small since treatments contained much lower biomass of these animals but, if the results are expressed as ammonium release per gram of animal biomass, the Collembola have nearly the largest effects of the groups examined (2.5 mg N g litter^{-1} g animal^{-1}). The overall effect of animal groups on ammonium-N release (N) in mg g litter^{-1} over a 6-week period relates linearly to animal biomass (B) according to the function:

$$N = 1.55B - 0.03.$$

Table 3.1. *Effect of animal groups upon the release of elements from F layer materials*[a]

	Control (without animals)	*Enchytraeids*	*Tomocerus minor*	*Orchesella villosa*	*Polydesmus angustus*	*Iulus scandinavius*	*Glomeris marginata*	*Lumbricus rubellus*
NH_4^+-N	0.03	0.02	0.10*	0.10*	0.38*	0.68***	0.54**	1.78***
NO_3^--N	0.002	0.002	0.004	0.004	0.006	0.008*	0.003	0.21***
Na^+	0.14	0.14	0.17*	0.19***	0.22*	0.18*	0.15	0.28***
K^+	0.13	0.13	0.20	0.17	0.29	0.44*	0.38***	0.46***
Ca^{++}	0.93	0.75**	0.84	0.81*	0.93	0.97	1.01	1.88***
Mean leachate pH	5.3	5.4	5.3	5.3	5.4	5.5	5.2	5.6
Wet weight of animals (g)	–	0.03	0.04	0.04	0.14	0.49	0.59	1.00
Number of animals	–	25	15	15	3	4	4	3

[a] Results expressed in mg g^{-1} dry wt of litter over a 6-week period. * p < 0.0~~0~~5, ** $p < 0.01$ and *** $p < 0.001$ for differences between animal treatments and controls; $n = 3$.

From Anderson, Ineson & Huish (1983*a*).

Such a function might form a basis for a process model through interactions with substrate quality (see below). This relationship also suggests that the taxonomic identity of the animals is not significant as a variable in relation to their biomass and activity. In the light of this we have chosen the millipede *Glomeris marginata* as a tool for modelling general animal effects, since this animal is particularly suitable for laboratory use.

The experiment described above was designed to simulate short-term, localized effects of feeding activities and the time scale was chosen to minimize nutrient immobilization through secondary production. The reproductive recruitment to these populations is longer term, and the effects of these changes will not normally affect local aggregations of individuals. The macroarthropod grazing effects, in particular, may be seen as a temporal perturbation, of variable intensity or duration, before the animals move on or the aggregation disperses, after which time the mineralization of nitrogen slowly returns to lower levels as discussed earlier. Collembola grazing had comparatively small effects on nutrient leaching from litter, but there was a five times larger transfer of nitrogen to animal biomass. This is a continuation of an effect seen for Protozoa and nematode grazing, where short generation times have the consequence that animal population levels closely follow local food supplies. Since weight specific metabolic rates and biomass turnover increase with decreasing body sizes, it may be that the faunal body size groupings of micro-, meso- and macrofauna reflect the increasing relative importance of indirect contributions to nutrient fluxes through animal–microbial interactions. Such relationships may be stabilized by the high spatial heterogeneity of the soil for invertebrates with a small body size (Fig. 3.3; Elliot, Anderson, Coleman & Cole, 1980; Couteaux & Pussard, 1983), while the macrofauna cause major changes to the microbial environment through litter comminution and the formation of soil aggregates (e.g. Jeanson-Luusinang, 1963).

Organisms: fungi

The selection of fungi by fungivores is a well documented phenomenon under laboratory conditions but less is known about the influence of fungi on the feeding activities of macrofauna. The fungal conditioning of litter appears to be a prerequisite for the onset of feeding by saprophagous animals, but the extent to which different species of fungi influence the scale and timing of effects requires investigation. If the dominant fungal species decomposing litter was a variable influencing the feeding activities of millipedes the broad, compartmental approach to investigating the effects of animals on mineralization processes suggested here would be invalidated.

Experiments were carried out in which oak leaf litter was autoclaved and then inoculated with one of six species of fungi: the basidiomycetes *Coriolus versicolor*, *Phallus impudicus*, *Marasmius androsaceus*, and *Flammulina velutipes*; *Mucor ramannianus* (Zygomycotina), and *Cladosporium herbarum* (Deuteromycotina). These were incubated for eight weeks at 20 °C before being transferred to the experimental chambers, which were allocated to treatments of 0 or 4 *G. marginata* per chamber (the optimum number of animals for demonstrating feeding effects in these systems). Ammonium-N leaching was then determined at intervals of one week over a period of nine weeks. Cumulative results for this period are summarized in Fig. 3.4. The data reflect the wide variation in

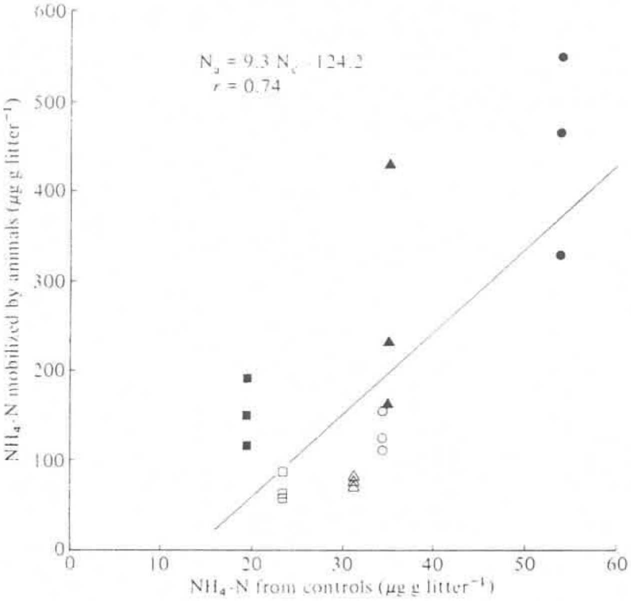

Fig. 3.4. The relationship between nitrogen mineralization by different species of litter-decaying fungi and the mobilization of nitrogen by millipede feeding activities. Oak leaf litter was inoculated with *Coriolus versicolor* (●), *Phallus impudicus* (▲), *Marasmius androsaceus* (■), *Mucor ramannianus* (○), *Cladosporium herbarum* (△) and *Flammulina velutipes* (□), and incubated for eight weeks at 20 °C before being transferred to microcosms and allocated to animal (4 *Glomeris marginata*) or control (no animals) treatments. Ammonium-N release was then determined weekly for nine weeks. Results are cumulative for this period.

ammonium-N release by the fungi, with *C. versicolor* achieving the highest levels of ammonium-N release (reflected by extensive structural breakdown of the litter), while *F. velutipes* showed extensive mycelial development on the litter but with little visual sign of catabolic activity. The response of these monospecific fungal cultures to animal grazing, as nitrogen mineralization (N_a), was significantly correlated ($P = 0.001$, $f = 16$) with nitrogen mineralized by controls (N_c) according to the function:

$$N_a = 9.3\ N_c - 124.2.$$

Thus, the effect of millipede feeding can be related to the activities of the fungus, and again transcends the specific identity of the organism involved. If this assumption is valid for mixed cultures then animal–microbial interactions in nitrogen mineralization can be predicted at the process level for a particular resource. We next consider resource as a variable.

Resource type

Litter (L), fermentation layer (F) and humus layer (H) materials were collected from three oak woodlands in Devon, and mineral element losses were compared for treatments with 0 and 4 *G. marginata* over a period of six weeks. Losses of sodium and potassium were increased in all cases but the effects were small in relation to the abiotic leaching processes which dominate the fluxes of these elements (Anderson *et al.*, 1983*b*). The effects of the animals on nitrogen mineralization were more marked (Table 3.2).

Leachates from the L-layer materials contained small concentrations of nitrate-N and the ammonium-N dominated nitrogen fluxes showed the expected enhancement by animals from about 10 to 15 times control levels. The F-layer material from Perridge and Brook Woods showed higher control levels of ammonium-N than the L-layer materials but the Stoke Woods material had similar leachate concentrations of ammonium-N and nitrate-N. The millipedes enhanced ammonium-N losses to about eight times normal levels in these experiments, while the enhancement of nitrogen as nitrate was insignificant. Another series of experiments with Stoke Woods F-layer material showed an enhancement of both forms of mineral-N, so that the ratio of ammonium-N to nitrate-N in leachate was similar in the control and animal systems. The H-layer material from Stoke Woods (Table 3.2) showed a dominance of nitrate-N in leachate from controls. This was maintained in the animal

Table 3.2. *Effects of* Glomeris *feeding on nitrogen leaching from different organic soil layers of three oak woodlands in Devon*

	Site:	*Stoke Woods*		*Perridge Wood*		*Brook Wood*	
	Treatment	*Control*	*Animals*	*Control*	*Animals*	*Control*	*Animals*
Litter layer (L)	NH_4-N	18.8 ± 5.7***	183.3 ± 10.3	23.7 ± 3.2*	251.1 ± 81.3	38.0 ± 19.5***	591.3 ± 69.6
	NO_3-N	1.6 ± 0.4*	3.5 ± 0.7	1.7 ± 0.4	3.7 ± 1.0	1.1 ± 0.5	5.5 ± 1.5
Fermentation layer (F)	NH_4-N	37.2 ± 8.4***	259.3 ± 24.3	217.9 ± 50.7**	513.9 ± 48.2	716.4 ± 194.4*	1333.5 ± 90.9
	NO_3-N	46.8 ± 28.2	16.4 ± 4.4	12.7 ± 9.5	4.4 ± 0.6	17.6 ± 5.2	61.2 ± 31.6
Humus layer (H)	NH_4-N	15.3 ± 2.1*	188.7 ± 50.7	131.0 ± 7.2***	214.7 ± 4.1	107.1 ± 6.5**	188.8 ± 17.5
	NO_3-N	116.1 ± 0.5	384.5 ± 50.3	2.3 ± 0.3	2.1 ± 0.2	13.9 ± 3.2	9.5 ± 2.0

Results are expressed as mean cumulative concentrations of mineral nitrogen (μg g dry wt litter^{-1} ± SE; $n = 3$) mobilized as ammonium-N or nitrate-N over a period of five weeks after the addition of four animals to the animal treatments. Values for controls (without animals) are shown for the same period of time. The experiments were incubated at 15 °C. Significant differences between animal treatments and controls are shown as *** ($P = 0.001$), ** ($P = 0.01$) and * ($P = 0.05$).

treatments, although the effects of the animals were larger on the ammonium-N fluxes (enhanced 12 times) than on the nitrate-N fluxes (enhanced three times). Ammonium-N was the main form of inorganic nitrogen in H-layer leachates from the other two sites and animals produced a similarly small enhancement of the F-layer materials.

It is often assumed that acid soils have a predominantly ammonium-N economy because nitrifying bacteria have higher pH optima than ambient conditions. However, there is increasing evidence, as illustrated by these experiments, that this is an overgeneralization (Robertson, 1982); e.g. it takes no account of heterotrophic nitrification which is carried out by a wide range of bacteria (including actinomycetes) as well as many fungi (Fochte & Verstraete, 1977). In order to investigate the enhancement of nitrification by animals, H-layer materials were collected from nine oak woodlands and treated as in the previous experiment. Nitrate-N concentrations in leachates were expressed relative to ammonium-N concentrations as the Relative Nitrification Index (RNI), calculated by dividing the nitrate-N concentration by the ammonium-N concentration (Robertson, 1982). The nine humus layer samples showed a wide range of RNI values, from less than 1 (ammonium-N dominance) to nearly 20 (nitrate-N dominance).

In all cases the animals reduced the RNI, by enhancing nitrogen losses as ammonium-N. However, it was also noted that the RNI before and after grazing was related to cation leaching. The correlations between RNI and animal-induced calcium leaching are highly significant ($r = 0.90$, $p < 0.001$) and it is possible to predict the release of calcium (C) in μg g litter^{-1} by animals by measuring the RNI (N) of controls using the function:

$$C = 11.5N + 3.6$$

We attribute this effect to the release of hydrogen ions as nitrification proceeds, releasing calcium from cation exchange sites. Organic matter is the main pool of exchange sites in acid soils and the effects of animals in enhancing nitrogen mineralization processes through their feeding activities can therefore have wider implications for ionic balances under these conditions.

Physical variables: temperature and moisture

Temperature is an important determinant of metabolic activity, and soil processes mediated by animals and microorganisms might be expected to show a predictable response to temperature changes within their physiological optima. A convenient expression of this response is the Q_{10} coefficient which indicates the fold-increase of a response over a 10 °C change in temperature. In temperate regions soil animal respiration (Reichle, 1971; Persson *et al.*, 1980) and the respiratory activity of soil and litter microorganisms (Anderson, 1973*b*; Schlesinger, 1977) show a Q_{10} relationship of 2 to 3 over the normal annual soil temperature range of about 5 °C to 20 °C. Many biological and physical parameters limit this response. Witkamp & Frank (1970) concluded that mineral element release effected by animal feeding activities would be expected to follow a $Q_{10} = 2$ relationship, but this would be an exception at higher temperatures under field conditions because of interactions between temperature and moisture. They observed that high temperatures and low moisture tensions inhibited microbial and millipede activities. Upon re-wetting, millipedes continued feeding at the same rates as before drying, but there was a characteristic flush of microbial activity and element release followed by immobilization during the subsequent growth phase of the microorganisms. Nutrient immobilization during the wetting and drying processes has been shown in the laboratory to be more significant than biotic processes for nutrient mobilization at high temperatures (Witkamp & Barzansky, 1968; Witkamp, 1969), but their significance for nutrient losses from leaf litter in the field remains to be quantified.

In the microcosm studies of Anderson *et al.* (1983*b*) the moisture content of the experimental material was never limiting but, even so, the temperature effect on potassium and calcium losses from animal treatments was much less than a twofold increase within a temperature range of 5 to 20 °C. This is consistent with the hypothesis that abiotic processes are mainly involved in the leaching of simple cations.

Both Clarholm *et al.* (1981) and Anderson *et al.* (1983*b*) found larger responses for nitrogen mineralization than can be predicted from simple temperature responses. Clarholm *et al.* (1981) did not differentiate between animal or microbial processes involved in these fluxes but recorded a fiftyfold increase in mineral nitrogen release between 5 °C and 20 °C from pine-forest soil material incubated at high moisture levels. Millipedes feeding on deciduous forest litter, however, produced a sevenfold increase in leaching of ammonium-N between 5 °C and 15 °C but only a threefold increase from 10 to 20 °C (Anderson *et al.*, 1983*b*). Whatever the causes of these effects, the consequences are that temperature responses are unpredictable with our current understanding of these systems. Increases in nitrate-N were small but significant and were attributed to enhanced nitrification under the warm and moist experimental conditions. This inflated effect of temperature on nitrogen mineralization is strongly indicative of indirect, synergistic interactions between animals and microorganisms, rather than direct metabolic transfers involved in ammonification. We conclude that far more information is needed on the temperature response of animal–microbial interactions for the formulation of any descriptive or predictive model of these processes.

In our current approach to quantifying the role of animal–microbial interactions under field conditions we recognize the problems of quantifying indirect and direct effects, particularly the turnover of animal biomass, at similar scales where the results can be combined into estimates of total nutrient fluxes. We are attempting to resolve these problems by using different scales of experimental systems, ranging from 0.5 m by 0.5 m field chambers for ecosystem studies down to laboratory microcosms for investigating microsite processes, towards formulating a multivariate model integrating faunal biomass, resource quality and temperature effects on animal–microbial interactions in nutrient fluxes.

Mechanisms of nitrogen mineralization and release

The role of soil animals in effecting the release of nutrients from decomposing plant materials is generally attributed to comminution increasing the susceptibility of simple cations to leaching or, particularly for limiting nutrients such as nitrogen and phosphorus, the reduction of microbial biomass through grazing. The nutrients in microbial tissues are then released over a longer time scale by the turnover of heterotroph tissues or by excretion (egesta and metabolic products) over a short time scale. The importance of metabolic nitrogen excretion as a process of nitrogen mineralization is emphasized in the reviews by Anderson *et al.* (1981) and Persson (1983).

Our interest in understanding the mechanisms of animal–microbial interactions in nutrient fluxes centres on the necessity for identifying the nutrient pools which are mobilized directly and indirectly by animal feeding activities, in order to develop quantitative models of the processes. Results of our experiments up to 1981 led us to advance the following hypothesis to account for the short term effects of millipedes on the release of nitrogen from leaf litter as ammonium (Anderson & Ineson, 1983).

It was assumed that during the early stages of litter decomposition net mineralization of nitrogen is low as a consequence of immobilization in fungal tissues. This is consistent with the low release of nitrogen from our ungrazed systems as well as with the general theory of the time course of litter decomposition (Swift *et al.*, 1979). In laboratory systems, without animals, the release of nitrogen from the fungal pool may not occur until carbon becomes limiting, as predicted by the C:N theory, but in natural systems animal feeding activities will accompany microbial colonization and the proliferation of facultative saprophytic fungi after leaf fall.

The mycelial growth form is very susceptible to disruption by animal feeding activities, more so than the unicellular bacterial thallus. Even so, 60 to 80% of a ^{14}C-label was assimilated from both bacteria and fungi by *G. marginata* (Anderson & Bignell, 1982; Bignell, personal communication). There is, however, extensive bacterial growth of both the residual litter flora and endogenous gut bacteria in the hind-gut of this millipede, so that the faeces contain several hundred times higher bacterial counts than the food litter (Anderson & Bignell, 1980; Anderson & Ineson, 1983) with increased abundance of ammonifiers as well as ureolytic and uricolytic forms. The importance of these bacteria in the nutrition of the animal has not been determined but the specific activities of these groups can be related to the degradation of amino acids in food materials and gut secretions, urea stored in fungal hyphae, and to uric acid excretory products of the animal which are voided into the gut (Anderson & Ineson, 1983). The end product of these processes is manifested by high concentrations of ammonium in the faeces of *G. marginata* (Bocock, 1963) and nitrogen immobilized in bacteria rather than fungi. We hypothesize that the low levels of fungal activity in these microsites together with carbon limitation of bacterial growth reduces nitrogen immobilization so that the ammonium is available for root uptake. Clarholm *et al.* (1981) found that addition of glucose to microcosms containing pine seedlings limited nitrogen availability to the plants because of increased microbial immobilization. The addition of glucose to our millipede-grazed systems had similar effects on ammonium leaching rates (Table 3.3).

The validity of these mechanisms, and the relative importance of direct and indirect effects of animals, resolves on the contribution of animal excretion to ammonium in the faeces and the mobilization of nitrogen from fungal tissues.

The excretory component of faecal nitrogen was investigated in experiments where *G. marginata* labelled with ^{15}N were allowed to

Table 3.3. *Nitrogen immobilization by glucose enrichment*

Treatments	*NH_4-N mobilized*	
(n = 4)	(μg g dry wt litter^{-1} week^{-1} ± SE)	
No animals, no glucose	2.03 ± 1.18	$P < 0.01$
Animals, no glucose	143.7 ± 30.3	
Glucose, no animals	5.90 ± 2.0	$P = 0.05$
Glucose plus animals	79.7 ± 25.5	

Oak leaf litter was incubated in chambers at 15 °C until week 3 when four *Glomeris* were added to animal treatments. Glucose additions (1% w. v.) were not made until week 11 when the animal treatments showed enhanced ammonium-N mobilization. Results are expressed as mean concentrations for weeks 12 and 13.

graze on non-labelled litter. Animals were labelled by feeding them on *Cladosporium herbarum* grown with double-labelled ^{15}N ammonium nitrate (Prochem, London) as the sole nitrogen source in a defined medium. The labelled animals were added to unlabelled leaf litter and the leachates analysed for mineral nitrogen and the ratio of $^{14}N:^{15}N$. It was calculated, based on the assumption that the animals were uniformly labelled, that 92.5% of the nitrogen released after adding the animals was derived from the litter and only 7.5% from excretion. Parallel experiments using ^{15}N-labelled litter and unlabelled animals showed the same general pattern. Thus, the short term significance of the animal effects lies predominantly in their indirect mineralization from the litter microbial pool, rather than the direct contribution through excretion.

Experiments were carried out in which litter was treated with nystatin to suppress fungal growth (Fig. 3.5). The experiment was monitored over 19 weeks at 15 °C and dilution series were prepared from litter controls, with and without nystatin, on five occasions during the course of the experiment and plated out on nutrient agar. Bacterial counts ranging from 2 to 7×10^8 colonies g litter^{-1} were not significantly different in the two treatments. The nystatin was effective in suppressing fungal growth since no fungi were isolated from the nystatin treated litter, whereas an average of 15×10^6 colony-forming units g litter^{-1} were found in the untreated controls. Unexpectedly, ammonium-N concentrations in leachates were similar from nystatin treated and untreated leaves even after animal addition (Fig. 3.5), suggesting that either the animals have similar effects in reducing bacterial or fungal immobilization of nitrogen (a conclusion supported by the ^{14}C-tracer experiments), or that the fungal nitrogen pool is insignificant in relation to nitrogen released from litter. But the net effect of feeding activities is that the animals assimilate only a small proportion of the nitrogen mobilized from the litter–microbial complex as a consequence of gut passage.

Conclusions

It would appear from the studies reviewed here that soil invertebrates have important roles in nutrient cycles of temperate grasslands and deciduous forests on base rich soils where their biomass equals or exceeds that of microorganisms and the decomposition rates of high quality litters are fairly rapid. In intensively farmed arable systems the applications of fertilizer usually override any necessity to account for animal or animal–microbially mediated effects on nutrient fluxes, though there is evidence for the importance of earthworms in

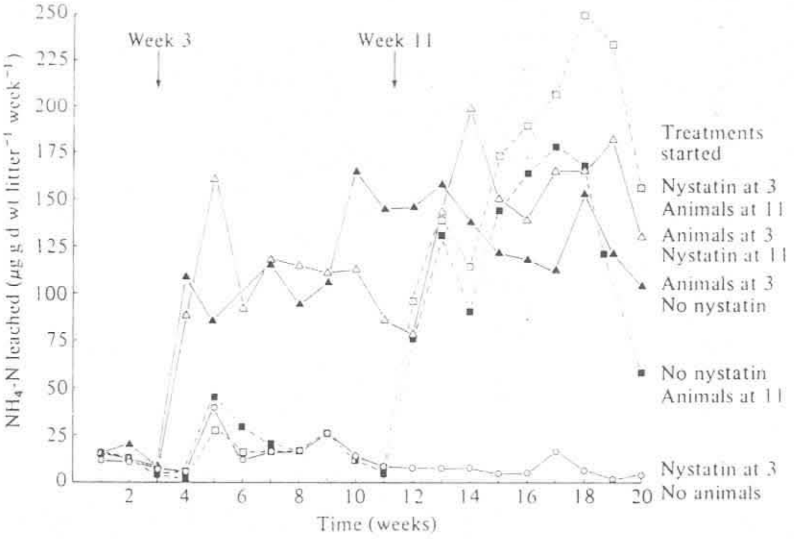

Fig. 3.5. The effects of nystatin treatments on ammonium-N release from litter by the feeding activities of *Glomeris marginata*. Chambers were set up containing oak leaf litter and treatments of 0 or 4 millipedes, with or without nystatin (50 μg ml^{-1}), were initiated at week 3 or week 11 as shown.

promoting the root growth of crops through their burrowing activities in minimum tillage systems (Edwards & Lofty, 1978).

In acid forest soils, particularly those developed under conifers, the immobilization of nitrogen and phosphorus in organic matter has economic implications for forestry practices and watershed management. Miller (1981) showed that in a pine plantation at Culbin Sands the application of 200 kg N ha^{-1} and a continued rate of mineralization of 4% only increased the available nitrogen from 60 to 63 kg ha^{-1} yr^{-1}. A shift in the mineralization rate for the soil organic pool (approximately 900 kg N ha^{-1}) from 4% to 4.5% would increase availability to 71 kg N ha^{-1} yr^{-1}, an amount roughly equivalent to the rate of immobilization resulting in nitrogen deficiency for the stand.

Net mineralization of nitrogen in a black spruce stand at Fairbanks (Alaska) is about 3% per annum of a 3070 kg ha^{-1} soil nitrogen pool (Van Cleve & Alexander, 1981). The data presented by Flanagan & Van Cleve (1977) for this site show that the bacterial and fungal standing crop (5.7 g m^{-2}) contains an insignificant fraction of the soil nitrogen pool, but the amount of nitrogen turned over through microbial productivity (117 g m^{-2}) amounts to about 6 g m^2 yr^{-1} or approximately 60% of the net annual mineralization reported by Van Cleve & Alexander (1981).

Both of these estimates of nitrogen mineralization, and the increase required at Culbin to support production, appear to be within the scale of the direct nitrogen transfers calculated by Persson (1983) for the Swedish Scots pine stand and the indirect effects demonstrated by us. It would therefore appear to merit serious consideration that animal–microbial interactions are functionally important in these sites and that manipulation of the soil fauna through management practices (Hill, Metz & Farrier, 1975; Lundkvist, 1977; Huhta, 1979) could provide a means of altering the balance of immobilization/mobilization processes.

We have little quantitative understanding of the role of soil fauna in mobilizing nitrogen from soil organic matter pools in acid deciduous forest soils. Most of the meso- and macrofaunal populations and feeding are associated with the litter and fermentation layers rather than with the organic humus horizons which contain the bulk of the immobilized nutrient pool. We see instead the soil fauna as agents of key processes determining the transfers of organic matter and mineral nutrient fluxes to the slower nutrient cycles associated with the humus pool. The feeding activities of animals not only enhance the existing patterns of nitrogen mineralization by the microorganisms, but also disrupt the time

Table 3.4. *Effects of* Glomeris *feeding activities on nitrogen and cation release from oak leaf litter and uptake by beech mycorrhizae–root systems in the field*

Treatments	*Minerals in leachate* (μeq *g dry wt litter*$^{-1}$ *week*$^{-1}$)				
	NH_4^{+1}	NO_3^-	Na^+	K^+	Ca^{2+}
No animals, no roots	3.84	0.13	0.36	0.33	1.61
Animals, no roots	7.50	0.09	0.61	0.49	1.78
No animals, roots	3.20	0.06	0.30	0.50	2.05
Animals, roots	3.61	0.04	0.63	0.33	2.11

scale of nitrogen mineralization in the surface litter layers so that nitrogen is released into solution in the sub-horizons where ectotrophic mycorrhizae are active.

The potential significance of these transfers has been demonstrated in experiments where mycorrhizal–root systems of oak trees have been introduced through ports in experimental chambers under field conditions. Ammonium-N released from the leaf litter by the feeding activities of millipedes was taken up by the root complex (Table 3.4) under conditions where the C:N ratio of the litter was approximately 100:1. Hence, the fauna are effecting transfers of nitrogen under conditions where net mineralization of nitrogen by microorganisms is thought to be insignificant.

The relative importance of the microbial and animal–microbial mediated processes is indicated by the results of the experiment shown in Fig. 3.1. Cumulative nitrogen mineralization over 15 weeks from the controls amounted to 3% of the total nitrogen capital (25.5 mg) in the litter compared with 9.7% mobilized through animal effects. Thus models of nitrogen mineralization from leaf litter which exclude the disruptive effects of animals on the time course of microbial decomposition processes must be considered unrealistic for temperate forest soils.

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